FISHES AND AMPHIBIANS FROM THE LATE PERMIAN PEDRA DE FOGO FORMATION OF NORTHERN BRAZIL

by C. BARRY COX *and* P. HUTCHINSON

ABSTRACT. The vertebrate fauna of the Pedra de Fogo Formation of northern Brazil includes a palaeonisciform fish *Brazilichthys macrognathus* gen. et sp. nov., which is placed in a new family, the Brazilichthyidae. Other fishes include fragments of ctenacanth and xenacanth sharks, edestid holocephalians, and dipnoans. Tetrapods include the archegosaurid amphibian *Prionosuchus plummeri*, which is compared with other archegosaurs. Its extremely long narrow snout suggests that the Pedra de Fogo Formation is of Late Permian age, rather than Early Permian. A large specimen of *Prionosuchus* is probably the longest amphibian currently known.

THE Pedra de Fogo Formation lies in the Maranhão-Piauí (or Parnaíba) Basin of northern Brazil, which covers parts of the state of Maranhão and adjoining states and which originated in the Siluro-Devonian. Permo-Carboniferous sediments deposited in this basin have, over the past thirty years, been given various names. The most common nomenclature today recognizes a Late Carboniferous Piauí Formation, which is overlain by the Pedra de Fogo Formation. The latter is overlain by the Motuca Formation, which is currently regarded as of Triassic age.

The Pedra de Fogo Formation was named after the small stream that runs through the area; the name is derived from the large amount of flint (firestone, or 'pedra de fogo' in Portuguese) which is found in its bed. The Formation was first recognized and defined by Plummer (1948), following the geological traverse of the Basin made by Plummer, Price and Gomes in 1946. In brief visits during 1945 and 1946, Price found fish and amphibian remains south of the township of Pastos Bons. The amphibian, which Price (1948) named *Prionosuchus plummeri*, was the first temnospondyl described from South America.

As Price concluded, the very elongate snout of *Prionosuchus* suggested that it belonged to the early group of long-snouted temnospondyls called archegosaurs, known from Permian sediments in Europe. The fish remains from the Pedra de Fogo Formation included the fin-spines of ctenacanth sharks, the teeth of xenacanth sharks, palaeoniscoid scales, coprolites and, at a lower level in the Formation, remains of the marattialian tree-fern *Psaronius*. Price (1948) concluded that the Pedra de Fogo Formation was certainly of Permo-Carboniferous age, and that it was most probably of Early Permian age.

The suggestion that *Prionosuchus* was of Early Permian age was of some interest, for it was the only Early Permian amphibian known from South America, and indeed one of the very few tetrapods known from the Early Permian of Gondwanaland (Cox 1974).

The Pedra de Fogo Formation therefore seemed to merit further investigation, and two visits to the Maranhão Basin were made. A reconnaissance in 1970 by L. I. Price of the Departamento Nacional de Producão Mineral, Rio de Janeiro, and J. Attridge of Birkbeck College, London, found a few fragments of amphibian. A larger party, consisting of the senior author and Attridge, together with Price and his assistant D. A. Campos, visited the area in 1972. The fish and amphibian remains described in this paper were found in the area where Price found *Prionosuchus*, east of the road between Pastos Bons and Nova Iorque (lat. 6° 35′ S, 44° 2′ W), and mainly up to 300 m east of those parts of the road that lie between 5·6 and 6·7 km south of the junction of that road and the main Highway BR-230 at Pastos Bons. A few fragments were also found east of a point 8·7 km

south of that junction. Geological maps today show the Pedra de Fogo Formation both to the east and to the west of Pastos Bons. However, both these areas were unproductive, despite aerial search for exposures, followed by ground search.

GEOLOGICAL BACKGROUND

Plummer (1948) stated that the Pedra de Fogo Formation, 10–20 m thick, was made up of alternating deposits of silt, limestone, and chert, the last predominating and forming beds and spherical concretions. The limestones contain oolites and pisolites, the silt layers contain the vertebrate fossils, and the chert beds contain edgewise, intraformational, fragmental conglomerates and, in some layers, large pieces of petrified wood. The chert also has an oolitic and pisolitic texture, and both Lisbôa (1914) and Plummer (1948) stated that the rocks were originally limestone and had later been changed to chert by chemical replacement, perhaps following deposition of a layer of volcanic ash over the region during the Early Cretaceous, when diabase was intruded into the earlier deposits.

Plummer (1946, fig. 2) drew a section in the Pedra de Fogo Formation 6·6 km south of the township of Pastos Bons, near the road to Nova Iorque. He showed it there to lie upon the upper part of the Floriano Formation (now included as part of the Piauí Formation), which consisted of grey marine shales interbedded with thin-bedded sandstones containing chert. Plummer stated that the Floriano Formation was of Late Pennsylvanian or Early Permian age. His figure showed that, in this region, the Pedra de Fogo Formation was unconformably

TABLE 1. Section through the upper part of the Pedra de Fogo Formation.

Height above base of Formation, in metres	Thickness in metres	
14·05		
	0·40	Basal conglomerate of Pastos Bons Fm.
13·65	1·45	Purple shale with subspherical concretions
12·20		Thin (0·002–0·005 m) layer of calcite
	0·30	Purple siltstone, as below
11·90		Thin (0·01 m) layer of calcite
	2·15	Purple siltstone, as below, including a 0·05 m layer of haematite with bone fragments
9·75		Thin (0·01 m) layer of calcite
	4·05	Finely bedded purple siltstone, with intercalations of greenish shale and of coarse sandstone with silica matrix. Occasional fragments of fossil wood.
5·70		
	1·60	Finely stratified greenish sandstone, as below.
4·10		
	0·30	Moderately stratified, light-coloured, poorly sorted sandstone.
3·80		
	2·90	Very fine greenish siliceous sandstone with cross-lamination
0·90		
	0·90	Fine siliceous purple sandstone.
0		
		Bed of large flints at bridge.

overlain by the Melancieiras Formation (now known as the Pastos Bons Formation, and considered as Middle-Late Jurassic in age; Pinto and Purper 1976). However, Plummer (1946, fig. 3) also described a section of the Pedra de Fogo Formation further east, between São Domingos and Benedito Leite, where he found that the Pedra de Fogo Formation was unconformably overlain by the dark brick-red sandstones of the Motuca Formation. He stated (1948, pp. 107–108) that the Motuca Formation was separated from the Pedra de Fogo Formation by an erosional unconformity, and that it was overlain by the Melancieiras Formation (now known as the Sambaiba Formation; Brito 1981). Plummer regarded the age of the Motuca Formation as uncertain, and it has been ascribed variously to the Late Permian or to the Triassic (Brito 1981; Medeiros, pers. comm., 1988).

A section was taken of the upper part of the Pedra de Fogo Formation, in the bed of the Pedra de Fogo stream where it ran under the Pastos Bons–Nova Iorque road at a point 6·6 km south of the junction of that road with Highway BR-230 (Table 1).

The vertebrate fauna of the Pedra de Fogo Formation comprises fin-spines of ctenacanth sharks and teeth of xenacanth (pleuracanth) sharks (Santos 1946), teeth of edestid holocephalians, dipnoan teeth, scales and cranial remains of palaeoniscoid fish, and the remains of temnospondyl amphibians (one of very large size). This fauna was found below a layer of fossiliferous haematite that occurred about 11·9 m above the base of the section. Most of the bones were free of haematite.

The levels of haematite and calcite, and the apparently lacustrine nature of the sediments, suggest a fresh-water environment of deposition. The ctenacanth and xenacanth sharks, which are elsewhere characteristic of fresh-water environments, is confirmatory evidence of this. The bone fragments are mostly badly worn, and the sediments had clearly been water-sorted and transported, fragments of similar size and density being found together. The overall impression is therefore one of deposition in the lower reaches of a river system. The large size of some of the vertebrates indicates that the body of water inhabited by these elements of the fauna must have been extensive, suggesting a deltaic environment including deep rivers or lakes.

The fin-spines and fish teeth from the Pedra de Fogo Formation are currently being studied by Dr Silva Santos of the DNPM. The description of the palaeoniscoid skull (below) is the work of the late Dr P. Hutchinson; the remainder of this paper is the work of the senior author (C. B. C.). Institutional abbreviations are: BMNH, British Museum (Natural History), London; DNPM, Departamento Naçional de Producão Mineral, Rio de Janeiro.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII
Order PALAEONISCIFORMES
Family BRAZILICHTHYIDAE fam. nov.

Diagnosis. As for genus.

Genus BRAZILICHTHYS gen. nov.

Type species. Brazilichthys macrognathus nov.

Brazilichthys macrognathus sp. nov.

Text-fig. 1

Horizon and locality. Pedra de Fogo Formation, state of Maranhão, N. Brazil. Found about 100 m east of the Pastos Bons-Nova Iorque road, about 6 km south of Pastos Bons.

*Holotype.* DNPM 1061-P, the only known specimen.

Diagnosis. Upper jaw margin strongly convex below orbit; teeth arranged in two series, the inner row composed of long, slightly recurved, conical teeth; median and lateral gulars almost half as long as the lower jaw. The genus is incompletely known, and this diagnosis must be regarded as provisional.

Description. The skull of *B. macrognathus* is represented by a single specimen, 80 mm long and 42 mm deep.

The dermal bones of the skull roof and opercular region are missing, but the other bones are well preserved, especially on the left side (Text-fig. 1A). The restoration (Text-fig. 1B) is based mainly on the left side of the specimen, but some additional details are derived from its right side.

The postorbital part of the maxilla is long and indicates that *B. macrognathus* had an inclined suspensorium. The part of the maxilla exposed below the orbit is extremely narrow, its dorsal edge being overlapped by the infra-orbital series and its ventral edge being separated from the upper jaw margin by a long premaxilla. The teeth of the upper jaw are arranged in two series: an inner series of eight or nine striated, conical teeth that are up to 6 mm long, and an outer series of more numerous teeth that are about 0·5 mm long. The larger teeth are terminated by small enamel caps similar to those described in *Pteronisculus* (*Glaucolepis*) by Nielsen (1942), and in *Nematoptychius* by Gardiner (1963).

The posterior and ventral edges of the orbit are bordered by two infra-orbitals. The anterior infra-orbital is slightly expanded at its anterior end (part of this bone was removed during preparation in order to expose details of the snout), while the posterior infra-orbital is broad and lunate. The dorsal edge of the orbit is bordered by a slender, curved element that extends anteriorly to meet the nasal. It is identified here as an infraorbito-supraorbital (dermosphenotic of other authors, e.g. Moy-Thomas and Dyne 1938; Gardiner 1963).
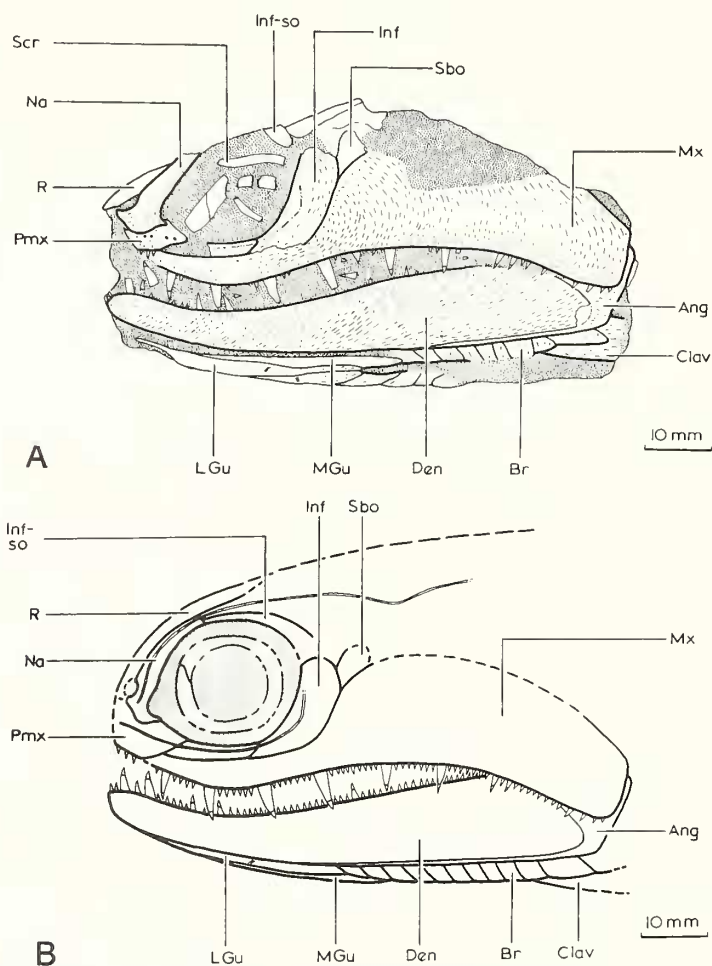
TEXT-FIG. 1. *Brazilichthys macrognathus*, gen. et sp. nov. Lateral view of skull, natural size. A, holotype, DNPM 1061-P. B, restoration of skull. Abbreviations: Ang, angular; Br, branchiostegal ray; Clav, clavicle; Den, dentary; Inf, infra-orbital (dermosphenotic); Inf-so, infraorbito-supraorbital; L Gu, lateral gular; M Gu, median gular; Mx, maxilla; Na, nasal; Pmx, premaxilla; R, rostral; Scr, sclerotic ring; Sbo, suborbital.

Objections to this view have already been put forward (Hutchinson 1975). It is also uncertain whether the infraorbito-supraorbital meets the posterior infraorbital, because the posterior edge of the latter bone is imperfectly preserved; however, comparison with other palaeoniscoids suggests that these bones did, in fact, meet to complete the posterior edge of the orbit.

The snout is composed of a rostral and paired nasals, premaxillae, and antorbitals. The rostral is identified as such in view of Patterson's (1975) conclusion that the median snout element in chondrosteans, identified as the post-rostral by many authors (e.g. Gardiner 1963, 1967 in palaeoniscoids; Hutchinson 1973 in redfieldiids and perleidids), is homologous with the rostral of holosteans and pholidophorids. Close to its ventral end, the nasal bears notches for the anterior and posterior nasal apertures. The premaxillae are unique among chondrosteans because they extend posteriorly almost to the level of the posterior orbital edges, and because they are separated at the tip of the snout. The antorbital is large and bears the ethmoid commissure of the infraorbital sensory canal. The antorbital branch is either absent or so poorly preserved that its course is not visible. The posterodorsal edge of the antorbital borders the orbital edge, and its posteroventral edge either butts against, or overlaps, the anterior ends of the anterior infra-orbital, the maxilla and the premaxilla. Its ventral edge bears the two types of teeth identified on the maxilla and premaxilla. The extreme anterior end of the antorbital is missing, so that the structure of the tip of the snout is unknown, but it appears likely that the antorbitals met at the midline of the snout.

There is an incompletely preserved suborbital wedged between the posterior infra-orbital and the dorsal part of the maxilla.

The lower jaw is long, and curves dorsally towards the symphysis. This curve is reflected in the shape of the edge of the upper jaw and does not appear to be due to post-mortem distortion. The teeth of the lower jaw are similar to those of the upper jaw, but are somewhat shorter. The angular extends along half the length of the lower jaw, but is almost completely overlapped on the lateral surface by the dentary, which is extremely thin posteriorly. There are three gular plates, which together are almost half the length of the lower jaw. The lateral gular plates bear short pit lines, but similar pit lines are not visible on the median gular. At least nine branchiostegal rays are present between the gular plates and the level of the posterior end of the lower jaw.

The known dermal bones of the skull bear an ornament of ridges and tubercles, and their distribution is indicated in Text-fig. 1.

[The form of the teeth and the elongated maxilla suggest that the family Brazilichthyidae may be related to the Permian family Acrolepidae (Gardiner and Schaeffer 1989): note suggested to senior author by Dr B. Gardiner, 1989.]

<div align="center">

Class AMPHIBIA

Order TEMNOSPONDYLI

Family ARCHEGOSAURIDAE

Genus PRIONOSUCHUS Price, 1948
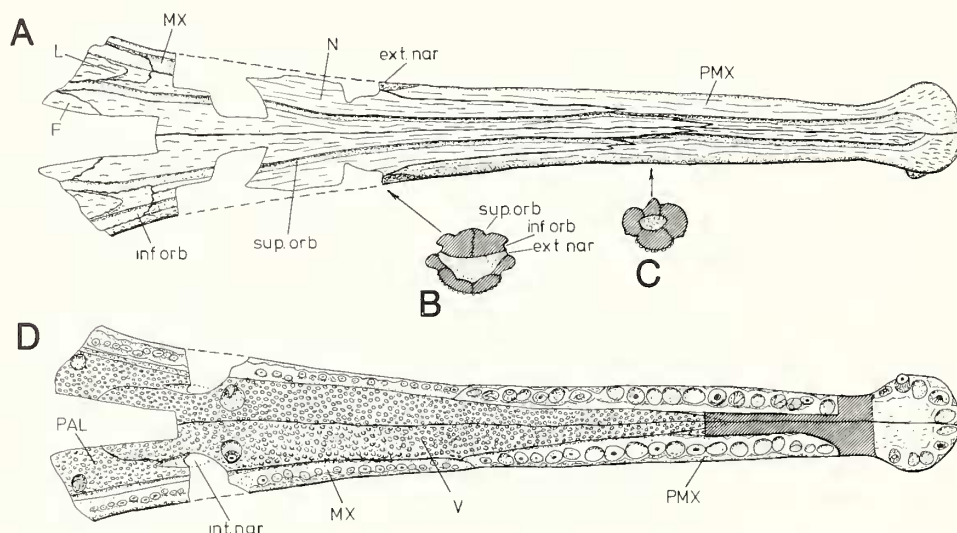
Prionosuchus plummeri Price, 1948

Text-fig. 2

</div>

Material. The genus was established by Price on the basis of a rostrum, a fragment of mandible and a femur (DNPM 320-R), all from the Pedra de Fogo Formation south of Pastos Bons. Price noted that the elongate rostrum resembles that of the archegosaur *Platyoposaurus*, but that it is proportionately much longer and more laterally compressed than that of *Platyoposaurus*. (The latter genus was originally named *Platyops* by Twelvetrees (1880) but, as noted by Lydekker (1889, p. xi), that name was preoccupied for a fish. Lydekker accordingly renamed the archegosaur *Platyoposaurus*.) Price also noted that the nasals, maxillae and palatines of the Brazilian specimen extend further forward than those of *Platyoposaurus*, and that the external nares are smaller and more laterally placed. He therefore established the new genus *Prionosuchus*. The rostrum of the holotype specimen is 345 mm long, and Price estimated that the complete skull would have been about 500 mm long.

Price collected scraps of two further rostra in the same area in a short visit in 1948 (DNPM 862-R, 863-R), and the 1970 reconnaissance collected further scraps, including a right mandibular ramus (DNPM 864-R) and two intercentra (DNPM 865-R). The following amphibian remains were collected during the 1972 expedition: BMNH R12000, the mid-portion of a rostrum; BMNH R12001, the posterior part of a rostrum; BMNH R12002, a median fragment of the frontal region of a slightly smaller skull; BMNH R12003, many fragments of a small skull; BMNH R12004, fragments of vertebrae, including pleurocentra and intercentra, and fragments of skull, and BMNH R12005, fragments of skull and post-cranial skeleton. The last specimen is nearly three times the size of most of the other amphibian specimens.

Description. Though the large specimen provides additional information on the anatomy of the posterior region of the skull and also contains portions of the rostrum, it is so fragmentary that the anatomy of the anterior part of the skull can be most reliably reconstructed using the fragments of the smaller skulls, and this is then used as a basis for estimating the size of the larger specimen.

Price's holotype specimen (DNPM 320-R) includes an almost complete rostrum, from the anterior tip back to a point slightly behind the internal nares. Anterior to the suture between the premaxilla and the maxilla, the rostrum is about 20 mm thick dorso-ventrally, and about 23 mm wide. Posterior to that suture, it widens to 31 mm at its posterior end but becomes only 17 mm thick dorsoventrally. The dorsal and the ventral surface are both flattened. The rostrum bears the anterior continuation of the supra-orbital sensory canal. The palatal surface of the vomers and palatines is covered with a fine shagreen of conical denticles. The expanded tip of the rostrum bears large teeth; immediately posterior to this, there is a constricted region bearing small teeth. Behind this constricted region, and as far back as the palatal portion of the premaxilla-maxilla suture, the teeth are of moderate size. Posterior to this suture, the teeth revert to smaller size. A pair of vomerine fangs and a pair of palatal fangs lie respectively anterior and posterior to the internal nares.

TEXT-FIG. 2. A, Dorsal and D, ventral views of the snout of *Prionosuchus plummeri* $\times \frac{1}{3}$, reconstructed from the type specimen (DNPM 320-R) and from the postero-lateral fragment (DNPM 862-R). B, C, Cross-sections of the snout at the positions shown, from specimen BMNH R12001. Abbreviations: F, frontal; L, lacrimal; MX, maxilla; N, nasal; PAL, palatine; PMX, premaxilla; V, vomer; ext.nar, external nares; int.nar, internal nares; inf.orb, infra-orbital sensory canal; sup.orb, supra-orbital sensory canal.

BMNH R12001 is a 105 mm long section of the middle portion of a rostrum of similar size. It differs from this region of the holotype only in that it is less flattened, being oval in cross-section, 24 mm thick and 34 mm wide, the palatal surface being convex (Text-fig. 2B, C). This suggests that the flattened form of the holotype was due to post-mortem crushing which collapsed the internal narial passage.

DNPM 862-R consists of two portions of rostrum, dorsoventrally crushed like the holotype. The anterior portion corresponds to the most posterior portion of the holotype, including the region of the internal nares and the posterior part of the external nares. The former appear to have been elongate and about 20 mm long; the dorsal and ventral regions of the specimen have therefore become broken apart from one another in this area. The palatal teeth are noticeably larger anterior to the internal nares than more posteriorly. The supra-orbital sensory canals are very well-developed, being up to 4 mm deep, and diverge posteriorly.

The more posterior part of DNPM 862-R is separated from the anterior part by a gap which ventrally appears to have been only a few millimetres wide. Ventrally, this part shows the posterior end of the internal

nares and, 18 mm behind this, the socket of the fang on the anterior end of the palatine bone. Dorsally, this part shows the nasal-frontal suture, the anterior end of the lacrimal bone, and two sensory canals. The more medial of these canals appears to be the posterior part of the supra-orbital canal. The more lateral canal is probably the infra-orbital sensory canal which, on BMNH R12001, can be seen to continue anteriorly and die out c. 30 mm anterior to the external nares.

BMNH R12000 and R12001 are uncrushed and show a series of cavities, filled with fine yellowish matrix, which extend through the snout. The posterior end of the rostrum fragment BMNH R12001 shows a section just anterior to the external nares (Text-fig. 2B); it shows a matrix-filled cavity extending from the external nares into the centre of the rostrum. The anterior end of the same specimen (Text-fig. 2C) shows a large central matrix-filled cavity, which presumably extended to the anterior end of the snout. Posterior to the external nares, the cavity formed the narial passage, which presumably ended at the internal nares. However, a fragment of the median portion of a small skull including the anterior part of the frontals (BMNH R12002) shows two smaller pairs of matrix-filled cavities extending posteriorly into the skull. In life, all these cavities were presumably filled with air and acted as flotation device for the head, rather like the cavities of the crocodilian skull.

Restoration and comparison. The fragments described can be used to produce a restoration of the anterior part of the skull of *Prionosuchus plummeri* (Text-fig. 2), which was about 380 mm long. Comparison of the sutural pattern of the snout of *Prionosuchus* with that of its closest known relative, *Platyoposaurus* (Text-fig. 3e) shows that the further elongation of the snout of the former has been achieved primarily in the region of the external nares. The nasals of *Platyoposaurus* end abruptly, at the level of the anterior end of the external nares. Those of *Prionosuchus* extend further forwards, gradually tapering to a narrow point, beyond which the snout is composed exclusively of the premaxillae. On the other hand, the lacrimals of *Platyoposaurus* nearly reach the external nares, while those of *Prionosuchus* hardly extend beyond the anterior end of the frontals, doubtless because of the great narrowing of the skull.

An estimate of the total skull length of *Prionosuchus* can be made by comparing it with that of *Platyoposaurus*. It would be possible simply to assume that the position of the naso-frontal suture was unchanged, and to enlarge a drawing of a *Platyoposaurus* skull until its width at this point was equal to that of the *Prionosuchus* skull. However, this may be an over-simple approach. The elongate snout of *Prionosuchus*, with its enlarged, spatulate tip, is identical to that found in the fish-eating gharial crocodiles of today. The narrowing of the snout reduces water-resistance when closing the jaws, and therefore allows the closure to take place more rapidly – an obvious advantage, especially when snapping at fish. Some of this advantage would be lost if the posterior end of the snout widened only gradually to match the width of the more posterior part of the skull, and this may be the reason why the snout of the gharial widens more abruptly. It seems likely that this would have been a factor also in the evolution of the snout of *Prionosuchus*, and the most posterior preserved part of its snout does indeed appear to curve outwards quite noticeably. In the reconstructed skull (Text-fig. 3F), it has therefore been assumed that the frontals do not project as far anteriorly as in *Platyoposaurus*, and the snout is shown as widening fairly abruptly. It is also possible that the coinciding anterior terminations of the lacrimal and of the frontal mark the level at which the skull narrowed abruptly into a snout dominated by the nasal, maxilla, and premaxilla. A reduction in the number of sutural joints in this latter structure would also increase its strength. It is possible that the degree of shortening of the immediately pre-orbital region that is shown in the reconstruction is incorrect, but there is at present no way in which this can be verified. As reconstructed in this manner, the total skull length of *Prionosuchus* based on these specimens would have been about 580 mm.

Post-cranial skeleton. A number of isolated amphibian pleurocentra and intercentra have been found in the Pedra de Fogo Formation, and show that *Prionosuchus* had a rhachitomous vertebral column similar to that known in other archegosaurs, such as *Archegosaurus* (Hofker 1928) and *Platyoposaurus* (Konzhukova 1955). The intercentra are up to 30 mm wide, and the pleurocentra are 20 mm high.

The large specimen of Prionosuchus. During the 1972 expedition, a much larger specimen of *Prionosuchus*

(BMNH R12005) was collected in the Pastos Bons locality. Though extremely incomplete, it included fragments of skull, vertebrae, ribs, scapulae, cleithra, clavicles, ilium, ischium, and femur.

The skull material includes fragments of the rostrum and palatal bones, both quadrates and parts of the margins of the orbits and otic notch. It is particularly interesting that one fragment shows the supratemporal bone entering the otic notch and so separating the tabular from the squamosal, as in *Archegosaurus*. The fragments show the expanded anterior end of the rostrum found in both *Prionosuchus* and *Platyoposaurus*, and the shagreen of palatal teeth characteristic of the former. The fragments also include a number of small, subcircular platelets of bone, up to 14 mm in diameter and 2 mm thick, with smooth, slightly convex under surfaces. Each platelet bears up to 30 denticles. They were probably embedded in the soft tissues of the mouth (for example, in the tissues overlying the interpterygoid vacuities), so that these areas, like the palatal bones, were denticulated and could grip the prey.

Despite the difference in size, there can be little doubt that this specimen belongs to *Prionosuchus*. The only part of it that is sufficiently complete to provide a basis for an estimate of its size when complete is the tip of the rostrum. This is 100 mm across, while that of the holotype specimen is only 35 mm across. As already mentioned, the snout of *Prionosuchus* is very like that of the modern fish-eating gharial crocodiles. Though the relative length of the snout of these crocodiles increases rapidly in early ontogeny, it remains almost constant from a skull length of 400 mm up to that of the largest specimen measured, 800 mm (data from Kälin 1933, tables II and III). It therefore seems reasonable to assume that proportions of *Prionosuchus* did not change greatly between the smaller (but definitely adult) specimens and the large specimen, in which the skull of the latter would have been about 1·6 m long.

Other archegosaurs, such as *Archegosaurus* and *Platyoposaurus* (Konzhukova 1955) had an elongate body and tail but small limbs. Though the skeleton of *Platyoposaurus stuckenbergi* that Konzhukova describes is incomplete, the first 9–10 vertebrae have a length approximately equal to $\frac{2}{3}$ the skull length. They are followed by another nine vertebrae with snout centra and ribs, with no sign of diminution in size towards the sacral region. There therefore seems little doubt that the body alone of such an archegosaur was considerably longer than the skull.

Prionosuchus certainly had small limbs, for the incomplete femora of the large specimen show that the complete bone could not have been more than 15 mm in diameter and 130 mm long. This indicates that it did not swim by means of enlarged, paddle-like limbs, but instead swam like a crocodile, by means of lateral undulations of the body and elongate tail. Wermuth (1964) has analysed the relationships between head, body and tail length in modern crocodilians. The largest gharial measured by him had a skull 0·83 m long, with a body 2 m long and a tail 2·65 m long – a total of nearly 5·5 m. Even if the snouts and body-plus-tail lengths of larger specimens of gharial or *Prionosuchus* were proportionately smaller than in specimens of intermediate size, there still seems little doubt that the large specimen of *Prionosuchus*, with a skull twice the length of that of Wermuth's largest gharial, must have had a total length greater than that of the gharial. There therefore seems little doubt that it was considerably larger than the longest amphibian presently recorded, *Eogyrinus attheyi* (Panchen 1972), which had an estimated total length of 4 m.

THE RELATIONSHIPS OF *PRIONOSUCHUS* AND THE AGE OF THE PEDRA DE FOGO FORMATION

As Price (1948) suggested, *Prionosuchus* is an archegosaurid: the great, slender elongation of the skull and the contact between the lacrimal and the frontal agree with Romer's (1947) definition of that family, in which he included three genera: *Archegosaurus*, *Melosaurus* and *Platyoposaurus*. Two other genera, *Bashkirosaurus* and *Collidosuchus*, were added by Gubin (1981, 1986).

The earliest member of the Archegosauridae is *Archegosaurus* itself (Text-fig. 3B). The type species, *A. decheni* (Hofker 1928; Whittard 1928), is from the ironstone nodules of the Lebach Group of the Saar region of Germany, of early Lower Permian age. Other specimens of *Archegosaurus*, named *A. ornatus* (Woodward 1905) and *A. kashmiriensis* (Tewari 1962) have been found in the Lower Gondwana deposits of Kashmir, which are probably also of Early Permian age.
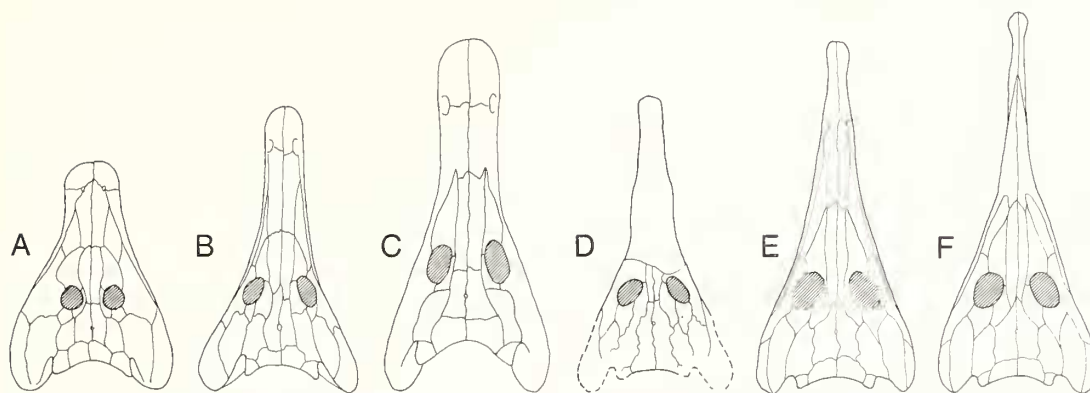
TEXT-FIG. 3. The skulls of archegosaurs, drawn to similar widths across posterior portion of the skull. A, *Melosaurus*, from Romer 1947, B, *Archegosaurus*, from Romer 1947. C, *Collidosuchus*, from Gubin 1986. D, *Platyoposaurus stuckenbergi*, after Efremov 1933 (his dorsal view, fig. 1, superimposed on his ventral outline, fig. 3). E, *Platyoposaurus watsoni*, after Efremov 1933. F, *Prionosuchus* (see text for details of reconstruction).

The other archegosaur genera, *Melosaurus*, *Bashkirosaurus*, *Collidosuchus*, and *Platyoposaurus*, are found in early Late Permian (Kazanian) deposits west of the southern Urals, in European Russia. The archegosaurs are found in Zones I and II of the deposits (which are numbered from the base upwards).

Melosaurus (Meyer 1860) was originally placed in the Archegosauridae because of its somewhat elongate preorbital region (Text-fig. 3A). However, this region is still comparatively short, being less than 50% of the total skull length, and is much wider than that of *Archegosaurus* (Text-fig. 3B). It is clearly not merely a juvenile archegosaur, as Hartman-Weinberg (1939) suggested, since skulls up to 400 mm long are now known.

Collidosuchus (Gubin 1986) has a snout whose elongation is intermediate between that of *Archegosaurus* and that of *Platyoposaurus* (Text-figs 3B–D). This is due in part, at least, to the appearance of a growth zone just anterior to the external nares, which consequently lie further back than in *Archegosaurus*, though not as far back as in *Platyoposaurus*.

Gubin had earlier (1981) described another Late Kazanian archegosaurid, *Bashkirosaurus*, but this specimen comprises only the median part of the skull from the orbits posteriorly. Rather surprisingly, Gubin does not mention this specimen in his later (1986) paper on *Collidosuchus*.

The genus which Lydekker (1889) renamed *Platyoposaurus* (see above, p. 565) was erected by Twelvetrees (1880) on the basis of a badly-damaged skull which he named *P. rickardi*. The snout of this specimen is lacking, and it seems unlikely that it shows any characters which would allow other specimens to be placed in this species. The name *Platyoposaurus rickardi* should therefore be applied only to the type specimen.

In 1884, Trautschold described a second species, *P. stuckenbergi*, based on a specimen which had an elongate, narrow snout and lower jaw. This specimen was redescribed by Efremov (1933), who also described a third species, *P. watsoni*, of which ten skulls were available, all from the same locality. Efremov stated that *P. watsoni* had a narrower snout than *P. stuckenbergi*, and this is also shown in his figures of the skulls (Text-fig. 3D). (His figure of *P. watsoni* in dorsal view was later used by Romer (1947, fig. 28) as his illustration of the genus *Platyoposaurus*.) However, Efremov also figured the lower jaw of this specimen of *P. stuckenbergi*, and this has a degree of narrowing and elongation very similar to that of *P. watsoni*. Efremov also stated that he could not locate the position of the external nares of *Platyoposaurus*, even approximately – presumably because, like those of *Prionosuchus*, these were narrow slits located on the sides of the snout.

Bystrow (1935) also gave figures of the skull of *P. watsoni*, but showed this as having a much wider snout than that shown in either of Efremov's figures, and with dorsally-directed external nares quite unlike those of the other specimens. However, this was reconstructed from fragments in the Paleozoological Institute in Stockholm, and is unlikely to be more reliable than Efremov's series of more complete specimens. Konzhukova (1955) has given the most recent account of *P. stuckenbergi*, basing this on a new specimen which includes much of the post-cranial skeleton but which unfortunately lacks the snout. A complete skull of *Platyoposaurus*, identified as *P. watsoni*, in the Museum of Comparative Zoology, Harvard (MCZ 1750) shows a snout shape identical to that of Efremov's reconstruction of that species, with no trace of the external nares in dorsal view.

There is clearly some uncertainty over the proportions of the snout in these two species of *Platyoposaurus* and, in view of the variable crushing of the cavities in the snout of *Prionosuchus*, it seems very likely that only one species is really present in the Russian deposits. It also seems unlikely (though not impossible) that two similar piscivorous species could co-exist with one another in the same environment. *P. watsoni* (Efremov) is therefore considered to be a junior synonym of *P. stuckenbergi*.

There can nevertheless be no doubt that the snout of *Prionosuchus* is even more elongate than that of the Russian forms (Text-figs 3E, F), and that it represents a new taxon of archegosaur. It is, however, debatable whether the Brazilian form should be placed in a separate genus from *Platyoposaurus*, or should instead be regarded as merely another species of that genus. Until a complete skull of *Prionosuchus* is found, it is impossible to know whether its degree of morphological difference from *Platyoposaurus* suggests recognition at specific or at generic level. For the time being, therefore, there is insufficient evidence to justify an alteration in the present taxonomic position.

Prionosuchus appears to represent a continuation of the archegosaur trend towards an elongate, narrow snout, and this implies that it is more advanced than *Platyoposaurus* in this character. Price, in his original description of *Prionosuchus* (1948), stated that he believed it was a primitive platyoposaurid. He gave no reasons for this statement, but his discussion of the diagnostic features of *Prionosuchus* mentions five characters in which it differs from *Platyoposaurus*: the greater anterior prolongation of the nasals and premaxillae; the narrow, widely-separated internal nares; the narrow, laterally-placed external nares; the much greater number of denticles on the palate; and the very pronounced lateral-line canals. Barberena (1972) concurs with Price in regarding *Prionosuchus* as a primitive platyoposaurid, and quotes these same characters as evidence. However, the first two characters seem to be results of the great elongation of the snout, which is surely an advanced character. The multiplication of the palatal teeth also seems to be an advanced character, while the depth of the lateral-line canals is variable within *Prionosuchus*. There therefore appears to be no reason for regarding *Prionosuchus* as a primitive platyoposaurid, but several characters instead suggest that it is more advanced than *Platyoposaurus*.

Barberena and Daemon (1974) have described a long-snouted temnospondyl from the Permian Rio do Rasto Formation of the Parana Basin, southern Brazil. Though they at first ascribed this form to *Platyoposaurus*, later discovery of the more posterior parts of the skull has shown that it is probably related to the trematosaurs rather than to the archegosaurs (Barberena pers. comm. 1976), though such a late date would be surprising for a member of that group, and the specimen does not show the conspicuous parallel vomerine tooth-rows characteristic of the trematosaurs.

In his original description of *Prionosuchus*, Price (1948) suggested that the Pedra de Fogo Formation was of Early Permian age. This was mainly because he felt that the general nature of the sediments and fauna was very similar to that of the Early Permian Red Beds of Texas, in which he had collected earlier. In addition, Price pointed out that the Pedra de Fogo fauna contained ctenacanths, which were then unknown from deposits later than Early Permian age. However, Bendix-Almgreen and Mahlzahn (1969) have since described a ctenacanth from the Kupferschiefer of Germany, which is of Late Permian age, even later than that of the *Platyoposaurus* specimens from Zone II of Russia. The other elements in the Pedra de Fogo Formation are of no use for dating purposes: xenacanths range from the Devonian to the Late Triassic (Patterson 1967), the dipnoan

fragments are too incomplete to allow of any identification even to family level, and *Brazilichthys* is isolated in a new family of actinopterygian fish. Though the fossil wood known as *Psaronius* is known only up to the Middle Permian of Europe, the Late Permian floras of Europe do not include petrification floras in which such wood would have been preserved. However, leaves of the *Pecopteris* type, considered to be those borne by *Psaronius*, have a much longer range in time (up to the Triassic), but the genus *Pecopteris* is so poorly defined that this range cannot be considered as reliable (W. G. Chaloner pers. comm.).

There is therefore little firm evidence on which to base an estimate of the age of the Pedra de Fogo Formation, other than that long-snouted archegosaurs are only known elsewhere from the Late Permian, which suggests a Late Permian age for the Formation. This in turn suggests that the Motuca Formation, which unconformably overlies the Pedra de Fogo Formation, is of Triassic age rather than Late Permian.

The re-assignment of the Pedra de Fogo Formation to the Late Permian is of additional palaeobiogeographical interest, in view of the fact that *Prionosuchus* had previously appeared to be one of the few tetrapods known outside Euramerica before the Late Permian. The realization of that fact provoked the suggestion (Cox 1974) that this was because Euramerica was still isolated from other continents until that time. However, it now appears that Euramerica had joined with Gondwana during the Carboniferous. Parrish *et al.* (1986) point out that all the occurrences of tetrapods prior to the Late Permian are found in equatorial to subequatorial palaeolatitudes, and that cool conditions for the Late Carboniferous to Early Permian are indicated by the distribution of coals, tillites and evaporites. They therefore suggest that climate was the principal cause of the absence of tetrapods from the higher southern palaeolatitudes of Gondwana until the Late Permian climatic improvement.

REFERENCES

ALDINGER, H. 1937. Permische Ganoidfische aus Ostgrönland. *Meddelelsen om Grønland*, **102**, 31–392.

BARBERENA, M. C. 1972. South American Late Paleozoic tetrapods. *Anais Academia brasiliensis de Ciencias*, *Supplemento* **44**, 67–75.

—— and DAEMON, R. F. 1974. A primeira ocorrência de Amphibia (Labyrinthodontia) na Formacão Rio do Rasto. Implicações geocronológicas e estratigráficas. *Anais do XXVIII Congresso Brasileiro de Geologia*, **2**, 251–261.

BENDIX-ALMGREEN, S. E. and MALZAHN, E. 1969. Uber neue oder wenig bekannte Elasmobranchier aus dem deutschen Kupferschiefer. *Notizblatt des Hessisches Landesamtes für Bodenforschung zu Wiesbaden*, **97**, 44–48.

BOY, J. A. 1972. Paläokologischen vergleich zweien berühmter Fossillägerstatten des deutschen Rotliegenden (Unterperm, Saar-Nahe-Gebiet). *Notizblatt des Hessisches Landesamtes für Bodenforschung zu Wiesbaden*, **100**, 46–59.

BRITO, J. M. 1981. Estratigráfia da Bacia do Parnaiba. *Anais do Academia Brasileiro de Geologia*, **53**, 529–549.

BYSTROW, A. P. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. I. Mitteilung. Schädcl dcr Stegocephalen. *Acta Zoologica, Stockholm*, **16**, 65–141.

COX, C. B. 1974. Vertebrate palaeodistributional patterns and continental drift. *Journal of Biogeography*, **1**, 75–94.

EFREMOV, J. A. 1933. Uber die Labyrinthodonten der U.d.S.S.R. II. Permische Labyrinthodonten des früheren Gouvernements Wjatka. 1. Neubeschreibung des Labyrinthodonten *Platyops stuckenbergi*, Trautschold aus den oberpermischen Ablagerungen des Flusses Kitjak, eines Nebenflusses der Wjatka. *Trudy Palaeontologii Akademii Nauk SSSR*, **2**, 117–164. [In German with Russian summary.]

GARDINER, B. G. 1963. Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bulletin of the British Museum (Natural History)*, (Geology), **8**, 255–325.

—— 1967. Further notes on palaeoniscoid fishes with a classification of the Chondrostei. *Bulletin of the British Museum (Natural History)*, (Geology), **14**, 143–206.

—— and SCHAEFFER, B. 1989. The interrelationships of lower actinopterygian fishes. *Zoological Journal of the Linnean Society*, **97**, 135–187.

GUBIN, Y. M. 1981. A new platyoposaurid from Bashkiria. *Paleontological Journal*, **1981**, 108–110.

—— 1986. New data on the archegosaurids of the East European platform. *Palaeontological Journal*, **1986**, 70–75.

HARTMAN-WEINBERG, A. P. 1939. *Melosaurus uralensis* H.v.M. an Upper Permian archegosaurid. *Problemy Paleontologii*, **5**, 20–31 [In Russian].

HOFKER, J. 1928. *Archegosaurus decheni* Goldf. *Palaeontologia hungarica*, **2**, 2.

HUTCHINSON, P. 1973. A revision of the redfieldiiform and perleidiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). *Bulletin of the British Museum (Natural History)*, (Geology), **22**, 233–354.

—— 1975. Two Triassic fish from South Africa and Australia, with comments on the evolution of the Chondrostei. *Palaeontology*, **18**, 613–629.

KÄLIN, J. A. 1933. Beiträge zur vergleichenden Osteologie des Crocodilidenschädels. *Zoologisches Jahrbuch*, **57**, 535–714.

KONZHUKOVA, E. D. 1955. *Platyops stuckenbergi*, Trautsch. – an archegosauroid labyrinthodont from the lower zone of the Cis-Uralian Upper Permian. *Trudy Palaeontological Institute*, **49**, 89–127. [In Russian.]

LISBÔA, M. A. 1914. The Permian geology of northern Brazil. *American Journal of Science*, **37**, 425–443.

LYDEKKER, R. 1889. *Manual of Palaeontology*, 3rd. ed. Vol. 2. Blackwood & Sons, Edinburgh and London.

MEYER, H. 1860. *Melosaurus uralensis* aus dem permischen System des westlichen Urals. *Palaeontographica*, **7**, 90–98.

MOY-THOMAS, J. A. and DYNE, M. B. 1938. Actinopterygian fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire. *Transactions of the Royal Society of Edinburgh*, **59**, 437–480.

NIELSEN, E. 1942. Studies on Triassic fishes from East Greenland, 1. *Glaucolepis* and *Boreosomus*. *Meddelelsen om Grønland*, **138**, 1–403.

PANCHEN, A. L. 1972. The skull and skeleton of *Eogyrinus attheyi* Watson (Amphibia: Labyrinthodontia). *Philosophical Transactions of the Royal Society of London, Series B*, **263**, 279–326.

PARRISH, J. M., PARRISH, J. T. and ZIEGLER, A. M. 1986. Permian-Triassic paleogeography and paleoclimatography and implications for therapsid distribution. 109–131. *In* HOTTON, N. *et al.* (eds). *The Ecology and Biology of Mammal-like Reptiles*. Smithsonian Institution Press, Washington and London.

PATTERSON, C. 1967. Family Xenacanthidae. 667. *In* HARLAND, W. B. *et al.* (eds). *The Fossil Record*. Geological Society, London.

—— 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London, Series B*, **269**, 275–579.

PINTO, I.D. and PURPER, I. 1976. Observations on Mesozoic Conchostraca from the north of Brazil. *Anais do XXVIII Congresso Brasileiro de Geologia*, **2**, 305–316.

PLUMMER, F. B. 1946. Report to Conselho Nacional do Petroleo, original M.S. in Departmento Nacional da Producao Mineral, Rio de Janeiro.

PLUMMER, F. B. 1948. Estados de Piauí e Maranhão. *Relatoria Anual do Conselho Nacional de Petroleo, Rio de Janeiro*, **1946**, 87–134.

PRICE, L. J. 1948. Um anfibio labirintodonte da Formação Pedra de Fogo, Estado do Maranhão. *Boletim de Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro*, **124**, 1–32.

ROMER, A. S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **99**, 1–368.

SANTOS, R. S. 1946. Duas novas formas de elasmobranchios do Paleozoico do Meio Norte, Brasil. *Anais do Academia Brasileiro de Ciencias*, **18**, 281–285.

TEWARI, A. P. 1962. On a new species of *Archegosaurus*, from the Lower Gondwana of Kashmir. *Records of the Geological Survey of India*, **89**, 427–434.

TRAUTSCHOLD, H. 1884. Die Reste Permischer Reptilien des Paläontologischen Kabinets der Universitäts Kasan. *Nouveaux Mémoires de la Société Impériale de Naturalistes de Moscou*, **15**, 3–39.

TWELVETREES, W. H. 1880. On a labyrinthodont skull (*Platyops rickardi*, Twelvetr.) from the Upper Permian cupriferous strata of Kargalinsk near Orenburg. *Bulletin de la Société Impériale de Naturalistes de Moscou*, **55**, 117–122.

WERMUTH, H. 1964. Das Verhältnis zwischen Kopf-, Rumpf- und Schwanzlänge bei den rezenten Krokodilen. *Senckenbergisches Biologiae*, **45**, 369–385.

WHITTARD, W. F. 1928. On the structure of the palate and mandible of *Archegosaurus decheni*, Goldfuss. *Annals and Magazine of Natural History*, **10** (1), 255–264.

WOODWARD, A. S. 1905. Permo-Carboniferous plants and vertebrates from Kashmir. II. Fishes and labyrinthodonts. *Memoirs of the Geological Survey of India. Palaeontologia Indica*, **11**, 10–11.

C. BARRY COX and P. HUTCHINSON

Division of Biosphere Sciences
King's College
Campden Hill Road, London, W8 7AH